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OCCURRENCE OF *TORVONEUSTES* (CROCODYLOMORPHA, METRIORHYNCHIDAE) IN MARINE JURASSIC DEPOSITS OF OAXACA, MEXICO

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ABSTRACT – IGM 9026 is a singular fossil collected at the beginning of the 20th century in an improperly documented site within the Tlaxiaco Basin, near to Tlaxiaco town, Oaxaca, Mexico. The age of the site was suggested as being early Cretaceous. This specimen is the holotype of *Plesiosaurus* (*Polypticodon*) *mexicanus*, which later was identified as a possible late Jurassic marine crocodylomorph of the family Metriorhynchidae, and consequently it was referred as ?*Cricosaurus mexicanus*. The present study provides a re-description of this fossil based on a microscopic analysis and the use of white and UV lights; these analyses led to the discovery of peculiar dental characters diagnostic of the genus *Torvoneustes*. This finding supports the re-classification of IGM 9026 under a new nominal combination as *Torvoneustes mexicanus*. Along the Tlaxiaco Basin, the fossil preservation mode and lithological composition observed in IGM 9026 only occur in the marine vertebrates recently discovered in Yosobé, a Kimmeridgian shale outcrop characterized by clay calcareous nodules that belong to the Sabinal Formation, near Tlaxiaco town. This peculiarity suggests that *T. mexicanus* could represent an additional element of the Kimmeridgian vertebrate assemblage recovered in this geological unit. The two nominal species of *Torvoneustes* were collected in Kimmeridgian marine deposits of England; hence, this finding expands the geographical distribution of *Torvoneustes* all along the Tethys Sea, from its Eastern/European to western/ Caribbean domains.

Keywords: *Torvoneustes*, *Plesiosaurus mexicanus*, hispanic corridor, Kimmeridgian, Tlaxiaco Basin, Sabinal Formation.

RESUMO – O exemplar IGM 9026 é um fóssil singular coletado no princípio do século 20 em um sítio pouco conhecido da Bacia Tlaxiaco, situado próximo a cidade de Tlaxiaco, Estado de Oaxaca, sul do México, cuja idade foi vagamente sugerida como do Eocretáceo. Originalmente, este único exemplar é holótipo do plesiossauro *Plesiosaurus* (*Polypticodon*) *mexicanus*. Mais tarde, ele foi identificado como um possível crocodilomorfo marinho do Jurássico Superior da família Metriorhynchidae, e portanto, foi referido como ?*Cricosaurus mexicanus*. O presente estudo proporciona uma nova descrição deste fóssil baseado em uma análise microscópica, uso de luzes brancas e UV, que levou à descoberta de caracteres dentários únicos neste exemplar, que coincidem com aqueles do gênero *Torvoneustes*. Este achado apoia a reclassificação de IGM 9026 a partir de uma nova combinação nominal como *Torvoneustes mexicanus*. Ao longo da Bacia de Tlaxiaco, o modo de conservação dos fósseis e a composição litológica observada em IGM 9026 somente se repetem nos vertebrados marinhos da Formação Sabinal, recentemente descobertos nas proximidades de Tlaxiaco. Esta peculiaridade sugere que *T. mexicanus* poderia representar um elemento adicional da associação de vertebrados fósseis do Kimmeridgiano da dita unidade geológica. As duas espécies nominais de *Torvoneustes* foram coletadas em jazimentos Kimeridgianos da Inglaterra, de forma que o presente achado amplia a distribuição geográfica do gênero ao longo do Mar de Tétis, desde a região Oriental na Europa até o seu domínio Ocidental no Caribe.

Palavras-chave: *Torvoneutes*, *Plesiosaurus mexicanus*, corredor hispânico, Kimmeridgiano, BaciaTlaxiaco, Formação Sabinal.

INTRODUCTION

Metriorhynchidae is a family of Middle Jurassic-Early Cretaceous marine crocodylomorphs (Wagner, 1858; Eudes-Deslongchamps, 1867-1869; Fraas, 1902; Andrews, 1913; Young, 1948; Pol & Gaparini, 2009; Cau & Fanti, 2011; Parrilla-Bel *et al*., 2013; Young *et al*., 2014; Herrera *et al*., 2015; Chiarenza *et al*., 2015). A number of peculiar adaptative features allowed the successful permanent marine life of this group. Among these, the most remarkable features are the presence of paddle-like forelimbs, hypocercal tail, osteoporotic like bone tissue, occurrence of large and highly

vascularised nasal salt glands draining toward the preorbital fossa, as well as the reduction of the olfactory tract and bulbs (*e.g*. Hua & Bruffenil, 1996; Fernández & Gasparini, 2000; Young *et al*., 2010; Herrera *et al*., 2013). Fossils of these crocodylomorphs have been collected in Europe, as well as in North and South America (*e.g*. Gasparini & Chong Díaz, 1977; Gasparini & Iturralde-Vinent, 2006; Buchy *et al.*, 2007; Wilkinson *et al.*, 2008; Young *et al.*, 2013a, b; Herrera *et al.*, 2015). Up to date, this family includes about 13 genera and 30–40 species gathered in two subfamilies, Metriorhynchinae and Geosaurinae, in which the Rhacheosaurini and Geosaurini constitute the more derived tribes, respectively (*e.g.* Young *et al*., 2013a, b).

Recently, an Aalenian–Bajocian (Middle Jurassic) metriorhynchoid, collected in the marine calcareous sandstones of the Snowshoe Formation exposed in Oregon, USA, was described by Wilberg (2015) under the name *Zoneait nargorum*. Although this author concluded that this ancient thalattosuchian is the sister taxon to Metriorhynchidae, the abundance and diversity of this family are still comparatively low in North America, where its occurrence is restricted to Mexico and Cuba.

Three incomplete and poorly preserved metriorhynchids have been reported from Cuba. Gasparini & Iturralde-Vinent (2001, 2006) concluded that the first is an indeterminate representative of *Geosaurus* Cuvier, 1824; the second is an indeterminate metriorhynchid; and the third is an indeterminate talattosuchian. Recently, Iturralde-Vinent & Ceballos-Izquierdo (2015) proposed that the first two specimens belong to *Cricosaurus* Wagner, 1858. Unfortunately, as the last authors noted, these taxonomic determinations are inconclusive because in addition to their poor preservation, these fossils suffered strong damages during their chemical preparation. The third of these Cuban specimens is an indeterminate Metriorhynchinae (Young & Andrade, 2009).

In Mexico the abundance and diversity of metriorhynchids is higher than in Cuba; therefore, this country has become increasingly important for the study of these ancient crocodylomorph. Since a little more than a decade, an increasing number of fossils of this family have been collected and carefully studied. Buchy (2007) provided a detailed overview of the metriorhynchids from Late Jurassic deposits of Mexico. These include *Cricosaurus vignaudi* Frey, Buchy, Stinnesbeck & López-Oliva, 2002, from the middle Tithonian deposits of La Pimienta Formation, near Mazatepec, Puebla; *Cricosaurus saltillensis* Buchy, Vignaud, Frey, Stinnesbeck & González, 2006, from Sierra de Buñuelas, near Gómez Farías, Coahuila; a fragmentary rostrum of *Dakosaurus* sp. from Kimmeridgian deposits of La Casita Formation, near San Juan de los Dolores, Coahuila (Buchy, 2008a); and other remains of indeterminate metriorhynchids collected in outcrops of La Casita and La Caja formations along Coahuila and Nuevo León.

Buchy (2008b) also identified an additional possible Jurassic Mexican metriorhynchid specimen, based on a resin mold of an intriguing fossil thought to be lost, which actually is cataloged as IGM 9026 into the Colección Nacional de Paleontología at Instituto de Geología, Universidad Nacional Autónoma de México (Figures 1–2). In fact, this specimen was collected and originally studied by Wieland (1910), who identified it as a plesiosaur that he named *Plesiosaurus* (*Polypticodon*) *mexicanus*. Unfortunately, the site where IGM 9026 was collected within Oaxaca State is not properly documented and its age was just vaguely designated as early Cretaceous. Afterward, Young *et al*. (2010, p. 852) suspected that this single and holotype specimen could belong to the genus *Cricosaurus*; therefore, they referred it as ?*Cricosaurus mexicanus* (also see Buchy *et al.*, 2013).

Recently, numerous fossil remains of Kimmeridgian marine crocodylomorphs have been collected in the Llano Yosobé, near Tlaxiaco, Oaxaca, Mexico (Alvarado-Ortega *et al*., 2014). IGM 9026 was meticulously examined during the comparative study of these new fossils. Such an exercise revealed some previously unreported tooth characters, which support the taxonomical re-assignation of IGM 9026 as part of the genus *Torvoneustes* Andrade, Young, Desojo & Brusatte, 2010, as well as the setting-up of a new nominal combination for this specimen. The aim of this study is to describe these newly discovered characters, to support the re-assignation of IGM 9026, and to explore some of the biogeographical implications of this finding.

MATERIAL AND METHODS

A comparative study of Jurassic marine crocodiles, including those newly discovered near Tlaxiaco (Alvarado-Ortega *et al*., 2014), established the mandatory review of IGM 9026 previously collected in the vicinity of this village of State of Oaxaca, Mexico. Given its unique nature and its designation as holotype of *Plesiosaurus* (*Polypticodon*) *mexicanus*, IGM 9026 cannot be prepared or altered in anyway. Therefore, in this study, IGM 9026 was observed under stereoscopic microscope and high resolution color and gray-scale photographs; these viewings were made under white light and ultraviolet light of short wave (254 nm), before and after its coating with ammonium chloride and magnesium-smoke. These procedures allowed us to recognize some structures that had not been observed before by other authors (Wieland, 1910; Buchy, 2008b).

Anatomical abbreviations. The anatomical nomenclature adopted in this study, as well as the anatomical abbreviations that appear in Figure 1, follow previous studies dealing with the anatomical description of metriorhynchids (*e.g.* Young *et al*., 2010, 2013a, b).

Institutional abbreviations. The fossil specimens used in this work with comparative purposes are included in the following scientific collections: **BRSMG**, Bristol City Museum and Art Gallery, Bristol; **IGM**, Colección Nacional de Paleontología, Instituto de Geología, Universidad Nacional Autónoma de México; **MACN**, Museo Argentino de Ciencias Naturales "Bernandino Rivadavia", Buenos Aires, Argentina; **MJCM**, Museo de Ciencias Naturales y Antropológicas "Juan Cornelio Moyano" Mendoza, Argentina; **MJML**, Museum of Jurassic Marine Life, Kimmeridge, Dorset, UK; **MLP**, Museo de La

Plata, La Plata, Argentina; **MOZ**, Museo Provincial de Ciencias Naturales "Prof. Dr. Juan Augusto Olsacher", Zapala, Neuquén, Argentina; **MUDE**, Museo del Desierto, Saltillo, Coahuila, Mexico; **UANL FCT**, Facultad de Ciencias de la Tierra, Universidad Autónoma de Nuevo León, Linares, Mexico.

Comparative material. The following specimens were used with comparative purposes in this work: *Cricosaurus araucanensis* (Gasparini & Dellapé, 1976): MLP 72-IV-7-1 (holotype), complete skull, postcranial skeleton; MACN N 64, anterior skull fragment; MACN N 95, complet skull and cervical vertebrae. *Cricosaurus lithographicus* Rusconi, 1948: MOZ-PV5787 (holotype), complete skull, jaws and postcranial elements. *Cricosaurus saltillensis* (Buchy, Vignaud, Frey, Stinnesbeck & González González, 2006): MUDE CPC 218 (holotype), posterior fragment of skull, jaws and first cervical vertebrae. *Cricosaurus vignaudi* (Frey, Buchy, Stinnesbeck & López-Oliva, 2002): cast of UANL FCT-R1 (holotype), skull, jaws and first cervical vertebrae. *Dakosaurus andinensis* Vignaud & Gasparini, 1996: MOZ- 6146 (holotype), skull and jaws. *Dakosaurus* sp.: MUDE CPC 201, rostral fragment (reported in Buchy *et al.*, 2008). *Purranisaurus potens* Rusconi, 1948: MJCM PV 2060 (holotype), posterior parts of the skull and a fragment of the right jaw.

SYSTEMATIC PALEONTOLOGY

Family METRIORHYNCHIDAE Fitzinger, 1843
Subfamily GEOSAURINAE Lydekker, 1889
Tribe GEOSAURINI Lydekker, 1889

Torvoneustes Andrade, Young, Desojo & Brusatte, 2010

Type species. *Torvoneustes carpenteri* (Wilkinson *et al*., 2008) Andrade, Young, Desojo & Brusatte, 2010. Originally, this was named as *Dakosaurus carpenteri* Wilkinson, Young & Benton, 2008; the actual authorships is in attention to recommendation 67B of the International Code of Zoological Nomenclature (International Commission on Zoological Nomenclature, 1999). The two specimens known of this species are from the upper Kimmeridgian marine deposits of the lower Kimmeridge Clay Formation, at Westbury, Wiltshire, England.

Additional species. *Torvoneustes coryphaeus* Young, Andrade, Etches & Beatty, 2013, from lowermost Kimmeridgian marine deposits of the lower Kimmeridge Clay Formation, at Studley Grange landfill, Lydiard Tregoze, Wiltshire, England.

Torvoneustes mexicanus (Wieland, 1910) comb. nov.
(Figures 1–3)

Holotype. IGM 9026, fragment of cranium including part of the maxillae and dentaries showing 12 teeth in oclussal position, and splenials forming the mandibular symphysis (Figures 1-2).

Type locality and horizon. Wieland´s (1910) locality, an unsuitably documented site in the north of the way to Putla, about 6 km to south-southwest from Tlaxiaco town, Oaxaca, Mexico (Figure 4). Originally, the age of this locality was designated as Neocomian (Wieland, 1910); later, Buchy (2008b) suggested that it is more likely to be Jurassic. Although the Wieland's locality is unprecise, in this work we suggest that IGM 9026 is a Kimmeridgian specimen from the Sabinal Formation deposits, near Tlaxiaco town, Oaxaca, Mexico (see discussion section in this manuscript).

Diagnosis. *Torvoneustes* species with a unique combination of characters, including robust teeth lingually curved with bicarinated conical crown, carinae bearing microscopic isomorphic denticles well defined (microziphodont condition); acute tooth crown apices; tooth enamel on basal two-thirds of the crown are heavily ornamented with long and thick apicobasal ridges that are uniformly spaced to each other; ridges near to the crown apex become short, drop-shaped tubercles randomly distributed, anatosmosed, and extended up to the carinae.

Description. We agree with the general description of bones preserved in IGM 9026 published by Buchy (2008b). The fragmented specimen is 84.94 mm high and 94.54 mm long. Teeth along the maxillae and dentaries are curved in posteromedial direction. Although, IGM 9026 is preserved in three dimensions and bones of both sides are present, the cortical surfaces of maxillae and dentaries are eroded and their external features are partially destroyed. In the left side of the specimen, this defect is so extensive that the large part of these bones and their teeth are not preserved (Figure 1D). In lateral view, the maxilla remain preserved is a long rectangular fragment of about 18.68 mm high. The cross sections of those bones are well exposed in posterior view; here, the maxillae are C-shaped and enclose a large ovoid nasal cavity (Figure 1C) previously identified by Buchy (2008b). A cross section of an empty dental alveolus preserved in the right maxilla is a large, ovoid hole encased in bone suggesting that this cavity is inclined forward as it happens with the tooth crowns preserved in this bone. In lateral view, the dentary fragment preserved is also a long rectangular structure, about 29.59 mm high. The reaction of bones preserved in IGM 9026 to UV light clearly reveals the presence of a deep surangulodentary groove (Figures 1B-C). In anterior view, the cross section of the right dentary is V-shape with two teeth exposed inside; the functional tooth is badly preserved while the other, a replacement tooth, preserves the fine details of its enamel tooth ornamentation (Figure 1E). The splenial bones can be seen in the cross sections exposed on the anterior and posterior views of IGM 9026. In posterior view, the right splenial is almost totally covered by recrystalized sediments. In right view, a small part of the left splenial is exposed (Figure 1D); this corresponds to the "possible fragment of the left mandibular ramus" identified by Buchy (2008b, fig. 3). These are flat high bones located medially to the dentaries, and sutured together along the midline to form part of the mandibular symphysis. The thecodont tooth implantation is exposed in the anterior and posterior surfaces of IGM 9026. A total of 12 teeth are preserved. Five maxillary and four dentary functional teeth are exposed in lateral view, on the right side

of the preserved skull (Figure 1B). In anterior and posterior views, the longitudinal sections of two functional dentary teeth are exposed, as well as a well-preserved replacement tooth (in the anterior view of these surfaces). The occlusion of teeth on dentary and maxillae follows an interdigitated pattern. The functional teeth of both bones are irregular in size but they seem to be separated by relative small and uniform interalveolar spaces, which seem to be close to one half of the alveolar length. In those teeth that expose the crown apex, this terminal tip is acute (Figure 2). It is possible to define the conic and curve shape of the robust teeth of IGM 9026 based on two facts. On one hand, the tips of all the exposed teeth are lingually bent and therefore covered by sediment or below the bones (Figure 1B). On the other hand, this curvature is obvious in the longitudinal section of the functional tooth preserved on the posterior broken surface of right dentary (Figures 1C-D). Based on the longitudinal section, the tooth has no constriction at the crown-root transition.

Tooth enamel covers the entire crowns. The anterior and posterior edges of the crown of both functional and replacement teeth have continuous cariane running from the bottom up to the crown apex. The tooth enamel on labial crown surface show two different ornamental elements; long and isolated apicobasal ridges aligned almost in parallel to each other that cover the basal two-thirds of the crown; in the apical end such ridges become short, discontinuous, and are randomly distributed, forming an anatosmosed pattern that extends up to the carinae; hence, the crown apex seems to be covered with small, drop-shaped, irregularly distributed tubercles (Figures 2A-B).

Along the entire lenght of the mesial and distal carinae, there are true denticles (Figure 2C). These denticles are regular in shape, size, and distribution; the lengths of their bases range around 142 μm and the denticle density (= # denticles/5 mm) is about 30. The features of these denticles show that IGM 9026 teeth have the microziphodont pattern only in the basal two-thirds of the crown. On the other hand, the superficial enamel ornaments reach the carinae of the crown apical end, showing the false-ziphodont pattern described by Andrade *et al*. (2010) and Young *et al*. (2013a).

Remarks. Buchy (2008b, p. 521) noted on "the architecture of the rostrum and constituting bones, as well as the tooth morphology" of IGM 9026 enough evidences to consider this as a crocodylomorph thalattosuchian belonging to subfamily Metriorhynchinae (family Metriorhynchidae). Later, Buchy *et al*. (2013, p. 18) claimed that "the dental and rostral morphology" of this specimen "is consistent with *Cricosaurus*: procumbent, uncompressed crowns with fine apicobasally aligned ridges; with a tubular snout; the dentary and maxilla parallel; and lacking denticulated carinae"; therefore this specimen was tentatively referred as ?*Cricosaurus mexicanus* (Young *et al.*, 2010, p. 852, tbl. A1). Unlike these previous observations, this paper shows that IGM 9026 has some ornamental characters with important implications for its subfamiliar and generic identification. IGM 9026 shows some remarckable characters considered in previous phylogenetic essays (characters 131-1, 135-2, 167-2, 168-2, 169-2 and 170-2, in Herrera *et al*., 2015; also see Young *et al*., 2012; Andrade *et al*., 2010; among others), which include the presence of: (i) alveoli longer than the nearby interaleveolar spaces (Figure 1B); (ii) a deep surangulodentary groove along the dentary bone (Figure 1C); (iii) bicarinated teeth (Figures 2, 3); (iv) denticles well defined and homogeneously distributed all along the carinae (Figure 2) [= true ziphodonty *sensu* Prasad & Broin (2002)]. Among metriorhynchids, the characters 1 and 2 are synapomorphies of the tribe Geosaurini, while 3 and 4 are present only in the most derived geosaurinis. According to Herrera *et al*. (2015), the tribe Geosaurini includes *Purranisaurus potens* Rusconi, 1948, from the upper Tithonian–lower Berriasian section of the Vaca Muerta Formation, Mendoza, Argentina; *Plesiosuchus manselii* (Hulke, 1870), from the upper Kimmeridgian to lower Tithonian deposits of England, and possibly also Spain (Ruíz-Omeñaca *et al*., 2010; Young *et al*., 2012); *Dakosaurus* (Quenstedt, 1843), represented by two nominal species and numerous ideterminate specimens from the upper Kimmeridgian to lower Berriasian marine deposits of Europe (England, France, Germany, Russia and Switzerland), South America (Argentina), and probably Mexico (see Vignaud & Gasparini 1996; Buchy, 2007, 2008a; Young *et al*., 2012; among others); at least three nominal species of *Geosaurus* from the Tithonian to Valanginian deposits of Europe (Debelmas & Strannoloubsky, 1957; Young & Andrade, 2009; Young *et al*., 2013b; among others); and two nominal species of *Torvoneustes* from the Kimmeridgian deposits of England and some late Oxfordian specimen from England referred to this genus (Andrade *et al*., 2010; Young *et al*., 2013b). IGM 9026 cannot belong to genus *Cricosaurus* because even though the species of this genus have non-, uni, or even bicarinated teeth, none of them have denticles along the carinae (= non-ziphodont condition). Unfortunatelly, *Purranisaurus* is not comparable with IGM 9026 because the teeth of this species are unknown (its inclusion within Geosaurini is based on diagnostic characters of the skull that are unknown in IGM 9026). *Dakosaurus* has macroziphodont teeth (denticles are distinctively large and naked-eye observable), whereas other geosaurins and IGM 9026 have microziphodont teeth (heights of these denticles are smaller than 300 μm) (*e.g*. Young *et al*., 2012). *Plesiosuchus manselii* and a putative unnamed close taxon, refered as "indeterminate Plesiosuchina" by Young *et al.* (2012, 2014a) and Chiarenza *et al.* (2015), lack the dual pattern of the tooth enamel ornamentation herein described along teeth of IGM 9026, in which the long apicobasal ridges present in the basal part of the crown becomes in the anastomosis of small drop-shaped tubercles on the crown apex; enamel is smooth all along the tooth crown in *Plesiosuchus manselii* while it is enterily cover with stout apicobasal ridges in the "indeterminate Plesiosuchina" (Young *et al*., 2012; Chiarenza *et al*., 2015). The strongly lateromedially compressed teeth with tri-faceted crown labial surface, already recorded in the species of *Geosaurus,* is easily differentiable from other Geosaurini taxa and IGM 9026, which have conical or slightly compressed teeth with no-faceted labial surfaces (Young & Andrade, 2009; Andrade *et al*., 2010).

Among geosaurinis, the tooth enamel ornamentations make of *Torvoneustes* a peculiar member. In this genus, the basal half-third of the crown shows conspicuous, long, and apicobasally

aligned ridges, whereas its crown apex is covered with short, discontinuous, and flattened tubercles that are stacked together displaying the "anastomosed pattern" described by Young *et al.* (2013b, p. 823). Now, the tooth enamel ornamentation of *Torvoneustes* is also known in IGM 9026 (Figures 2A-B); consequently, this specimen is reassigned to the genus *Torvoneustes*. Similar tooth enamel ornamentations are present in at least two teleosaurids, *Machimosaurus* von Meyer, 1837, and *"Steneosaurus" obtusidens* Geoffroy Saint-Hilaire, 1825; in these semiaquatic crocodylomorphs, the tooth carinae are heterogeneous because its denticles, although true and isomorphic, are poorly defined and discontinuously distributed (Young *et al*., 2014b, 2015). The carinae pattern found in these teleosaurids contrasts with IGM 9026, because in the latter the homogeneous carinae have true, well-defined, isomorphic and continuously distributed denticles.

Today, the genus *Torvoneustes* is known by two Kimmeridgian species from the lower Kimmeridge Clay Formation, England, as well as by some Late Oxfordian specimens from England tentatively referred to this genus and that unfortunately lack teeth (Young, 2013). The Kimmeridgian type species are *T. carpenteri* and *T. coryphaeus*. Three dental characters are different in these two species. In *T. carpenteri* the tooth crowns are slightly curved backward, slightly laterally compressed (about straight and circular in cross section), and the anastomosed pattern of enamel ornaments in the crown apex extends onto the carinae (Young *et al*., 2013b). Conversely, in *T. coryphaeus* the tooth crowns are notably curved, strongly laterally compressed, and its crown apex has a smooth area between the carinae and the anastomosed pattern of tooth enamel (Young *et al*., 2013b). Although the cross sections of the teeth are unknown in IGM 9026, this specimen shows a distinctive combination of the other two characters; its teeth are strongly curved (as in *T. coryphaeus*) and the tooth enamel ornamentations form an anastomosed pattern reaching the carinae (as in *T. carpenteri*). Additionally, IGM 9026 differs from these English species in the tooth apex acuteness; teeth tips in IGM 9026 are particularly sharp while in *T. carpenteri* and *T. coryphaeus* these are rather blunt. On the other hand, in IGM 9026 the denticles that shape the microziphodont pattern in the basal part of the teeth are well defined while in *T. carpenteri* and *T. coryphaeus* these denticles are poorly defined. Displayed these differences, herein IGM 9026 is recognized as a new species of *Torvoneustes*, which is named under a new nominal combination as *Torvoneustes mexicanus*.

Although some of the distinctive tooth characters of *Torvoneustes* could be linked to the ontogeny, up to date, the number of specimens of the three species of *Torvoneustes* is extremely low; hence, there are no enough data to characterize the possible ontogenetic changes on teeth of these organisms. In this context, the tooth morphological differences found in the specimens of *Torvoneustes* cannot be minimized or ignored because these may have real value to identify species. Therefore, considering the actual knowledge on the tooth morphological diversity of this genus, its three nominal species, including *Torvoneustes mexicanus* comb. nov., are enough different to each other to be considered as valid species.

DISCUSSION

The losts Wieland's site

Wieland (1910, p. 361-362) provided some clues about the collection site of specimen IGM 9026, which occurred in "in March 8th of 1909 by at a point north of the way to Putla town, about 6 km south-southwest from Tlaxiaco town, Oaxaca" (Buchy, 2008b). Although the age of this specimen was originally considered as Cretaceous, it was later considered more likely to be Jurassic (Reynoso, 2006; Buchy, 2008b; among others). Given this geographical and temporal uncertainty, the site of IGM 9026 was considered lost. Fortunately, two additional elements recovered in the present work facilitate the recognition of this lost site.

On the one hand, both nominal species previously described of *Torvoneustes* are restricted to the Kimmeridgian age; this suggests that *T. mexicanus* may be of the same age. On the other hand, the recently paleontological prospection along Tlaxiaco Basin has provided a more detailed picture about the geology near the Tlaxiaco town (Alvarado-Ortega *et al*., 2014; Barrientos-Lara *et al*., 2015). The Figure 4 presents a geological map of the south-southwest area of Tlaxiaco town, showing that the Kimmeridgian geological unit corresponds to the Sabinal Formation where numerous remains of marine invertebrates and vertebrates (including metriorhynchids) have been collected. Regarding the possible Kimmeridgian age of *T. mexicanus* and those "6 km south-southwest from Tlaxiaco town" reported by Wieland (1910), it is easy to locate the potential collection site of IGM 9026 along the outcrops of the Sabinal Formation, into a small area of this map. Hence, the collecting site of IGM 9026 is potentially within an area smaller than one km^2, located just 3 km southwest of La Lobera and Yosobé, two rich fossiliferous sites recently reported by Alvarado-Ortega *et al*. (2014) and Barrientos-Lara *et al*. (2015).

It is also remarkable that along the entire Tlaxiaco Basin, the tridimensional preservation and cream-coloured clay matrix of IGM 9026 are similar to those found in some marine vertebrate specimens from the Llano Yosobé. Recently, Alvarado-Ortega *et al.* (2014) described this site near Tlaxiaco town and reported the finding of numerous Kimmeridgian invertebrate and vertebrate fossils preserved into peculiar calcareous nodules present in a 30 m thick section belonging to the Sabinal Formation. Outcrops of this geological section extends along the ancient Tlaxiaco-Putla road where Wieland (1910) collected the specimen IGM 9026.

Biogeographic importance of *Torvoneustes mexicanus*

The Hispanic Corridor is a marine pathway between the western Tethys Sea and Pacific Ocean opened during the Jurassic breakup of the supercontinent Pangaea (Damborenea, 2000; Damborenea *et al*., 2013). The opening of this corridor was an important paleogeographic event that impacted on the composition and distribution of the Jurassic and Cretaceous

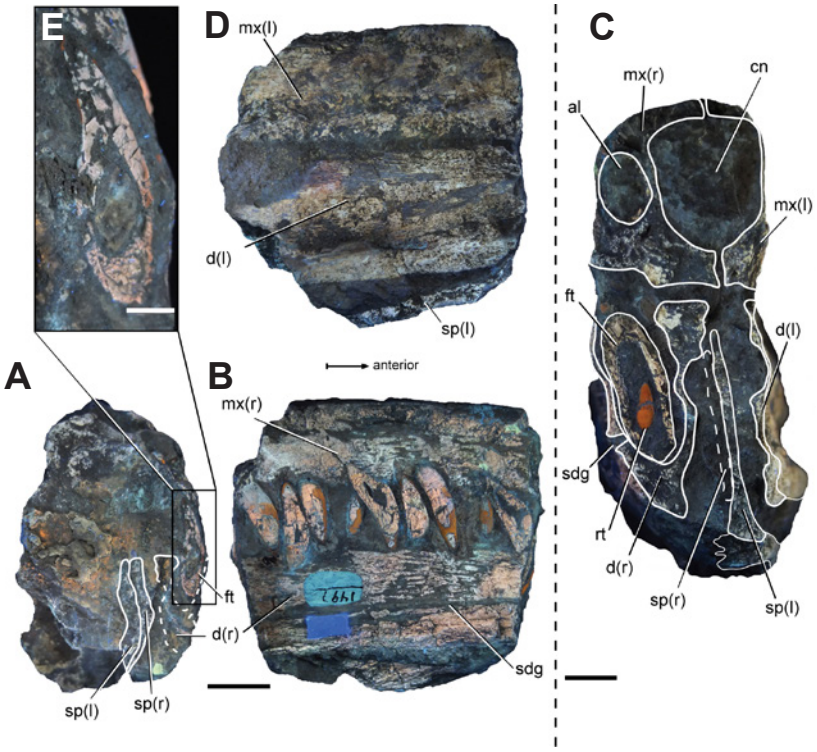

Figure 1. A–E, IGM 9026, *Torvoneustes mexicanus* comb. nov. under UV light in posterior (**A**), right lateral (**B**), anterior (**C**), left lateral (**D**) views. **E**, close-up of the cross section of a dentary tooth. **Abbreviations: cn**, nasal cavity; **d**, dentary; **fm**, functional tooth; **mx**, maxilla; **sdg**, surangulodentary groove; **rt**, replacement tooth; **sp**, splenial; **al**, alveolus. Arrows show the anterior end of the specimen. Scale bars: A-B, D = 20 mm; C = 10 mm; E = 5 mm.

marine faunas because this was an important migration route. Its effects on the biogeographical patterns of some benthonic invertebrates began in the Early Jurassic (*e.g.* Boomer & Ballent, 1996); however, it has influence on the distribution of pelagic invertebrates until the late Middle or even Late Jurassic (Damborenea, 2000; Aberhan, 2001). This corridor also was a dispersion route for many pelagic marine reptiles (plesiosaurs, ichthyosaurs, and marine crocodylomorphs) since the Oxfordian (Gasparini & Iturralde-Vinent, 2006).

During the Jurassic, the Tlaxiaco Basin was a depocenter for continental and marine sediments. To the northeast, it was connected to a wide Mexican epicontinental sea and to the Gulf of Mexico, which then constituted the Western Domain of the Tethys Sea. Marine deposits in this basin also were fed from the west by the Pacific Ocean. Thus, the marine fossils of the Tlaxiaco Basin represent an important expression of the Jurassic paleodiversity and the biogeographic processes attributed to the Hispanic Corridor. The discovery of marine vertebrates along this basin and the review of its fossils (as the specimen IGM 9026) open the opportunity to lern more about such historical patterns and processes (Alvarado-Ortega *et al*., 2014).

Up to now, the metriorhynchids known from localities along the Hispanic Corridor include two Oxfordian specimens of *Cricosaurus* and one indeterminate metriorhynchine from the Jagua Formation in Cuba (Iturralde-Vinent & Ceballos Izquierdo, 2015); the Mexican Kimmeridgian-Tithonian metriorhynchids mentioned above that belong to *Cricosaurus*, *Dakosaurus*, and a large number of indeterminate fossils. To this list we can now add *Torvoneustes mexicanus* nov. comb. that is described in this paper. This last record is important because *Torvoneustes* represents an additional Kimmeridgian faunistic element in the Hispanic Corridor that complements our knowledge on the temporal and geographical distribution of Jurassic marine vertebrates.

The recently description of *Zoneait nargorum* in Oregon, and the discovery of its sister relationship with the family Metriorhynchidae (Wilberg, 2015), opens the possibility that this family could be better represented than previously thought in North America since the Middle Jurassic. However, the comparision of the taxonomical diversity of these crocodiles along Europe, South America, and North America is still highly contrasting. In Europe (Germany, Spain, France, England, and Italy), metriorhynchid diversity is the largest and includes at least 22 species of 12 genera, which began to be described since the first half of the 19th century (*i.e.* Cuvier, 1824). One hundred and fifty years later, Gasparini & Dellapé (1976) launched the formal study of metriorhynchids in South America (Argentina and Chile), where now are known by six species of four genera. The study of metriorhynchid fossils began only 28 years ago in North America, when Ferrusquía-Villafranca & Comas (1988) described the first metriorhynchid discovered in Mexico, based on specimens that today seem to be lost. Before the report on the fossil bearing sites near Tlaxiaco (Alvarado-Ortega *et al*., 2014), only two species (two nominal species of *Cricosaurus*) and two genera (including the indeterminate specimens of *Dakosaurus)* were known all along North America.

Although the contrasting regional metriorhynchids diversity noted above may be a bias caused by different

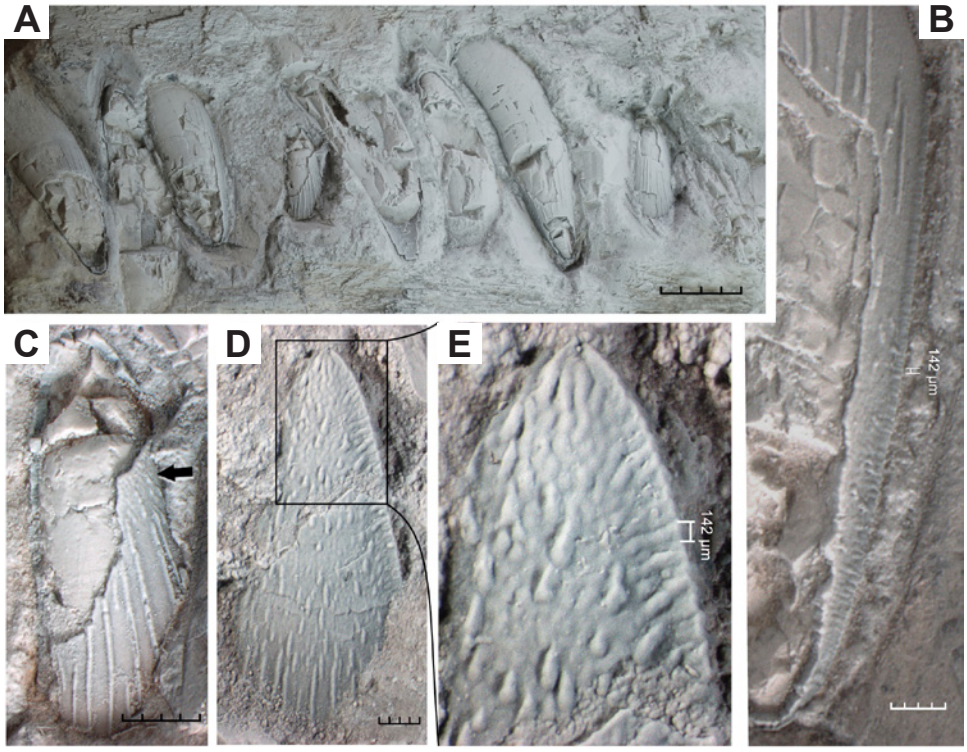

Figure 2. A–E, dental details of IGM 9026, *Torvoneustes mexicanus* comb. nov.. **A**, general view of the right teeth; **B**, maxillary tooth showing the microziphodont condition of the carinae (microscopic isomorphic denticles well defined and evenly distributed); **C**, dentary tooth showing both tooth enamel ornamentations, the long thick apicobasal ridges at the base and the short, randomly distributed, and anatosmosed drop-shaped scabs, extended up to carinae toward the crown apex (indicated for the black arrow); **D**, replacement dentary tooth showing both tooth enamel ornamentations (compare to C) and the acute shape of the crown tip; **E**, close-up of C showing the short, randomly distributed and anatosmosed drop shaped tubercles on the crown apex extended up to the tooth borders and the false ziphodont of the carinae in this section. Scale bars: A = 10 mm; B, D = 1 mm; C = 2 mm; E = 142 µm.

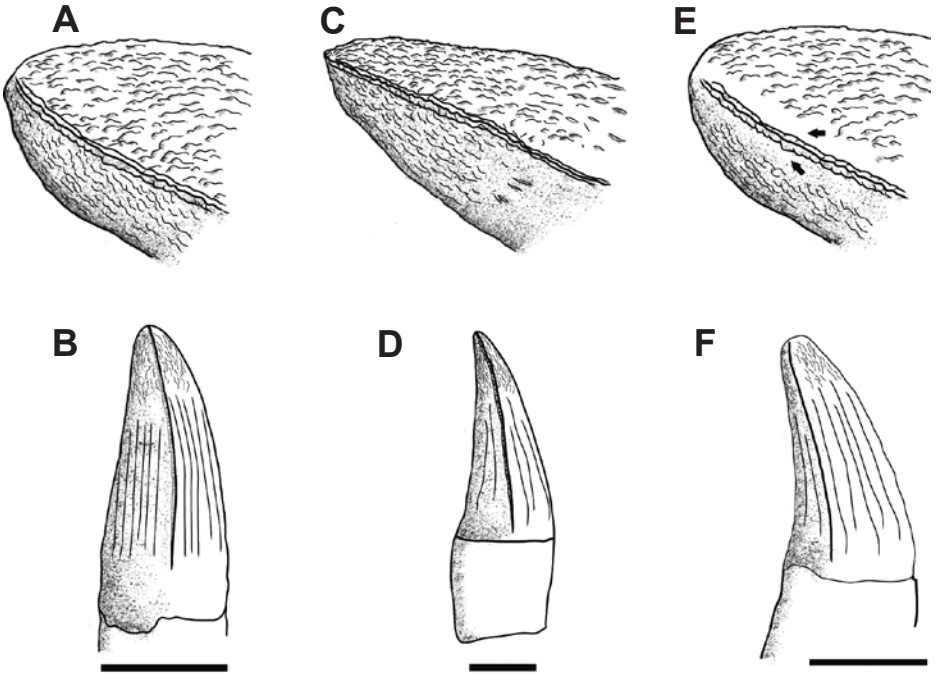

Figure 3. Schematic line drawings of teeth showing the distinctive dental characters of the three nominal species of *Torvoneustes,* including the accutness of crown apices, the distribution of tooth enamel ornamentations, and the curvature and robustness of the tooth crow. **A-B**, *T. carpenteri*, based on BRSMG Cd7203 illustrated by Young *et al*. (2013a, fig. 26) and Chiarenza *et al.* (2015, fig. 4); **C-D**, *T. mexicanus* comb. nov., based on IGM 9026; **E-F**, *T. coryphaeus*, based on MJML K1863 illustrated by Chiarenza *et al*. (2015, fig. 4). Arrows show the unornamented surface in the tooth crown apex between the carenae and the small anatosmosed drop-shaped scabs. Scale bars: A-B, E-F = 10 mm; C-D = 5 mm.

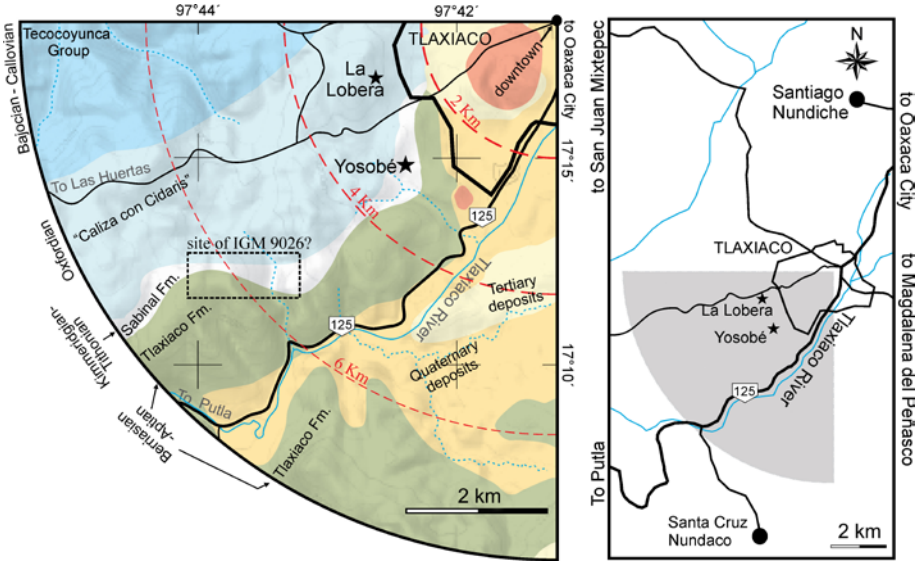

Figure 4. Map of the Tlaxiaco area showing different geological units outcropping in this area of Oaxaca State, Mexico, as well as the potential area where the specimen IGM 9026 was collected by Wieland in 1910 (based on Alvarado-Ortega *et al*., 2014, fig. 3; Servicio Geológico Mexicano, 2000).

sampling effort in Europe, South America, and North America, a pattern on the geographical distribution of the metriorhynchids is manifest. There are three groups, being two with a restricted regional distribution, one only recognized in South America and other only present in Europe. The third group is widely distributed metriorhynchids, from Europe to South America. The occurrence of *Cricosaurus* and *Dakosaurus* into the Caribbean region of North America plays the pivotal role of the Hispanic Corridor in the dispersion of the metriorhynchids. The present finding of *Torvoneustes* in Mexico reveals a fourth and intermediate metriorhynchid group, which includes taxa that could survive along the entire domain of the Tethys Ocean but were incapable to go beyond the Caribbean region. In this scenario, the Hispanic Corridor also worked as an effective barrier that prevented the dispersion of some metriorhynchids from the Tethys Ocean to the Paleopacific Ocean. We acknowledge that these observations are incomplete, and the proposition of a biogeographical hypothesis of this extinct clade should await the formal study of the metriorhynchids newly discovered in the Yosano Plain (Barrientos-Lara, 2016). This study will also include different vertebrate taxa with European affinities, such as the plesiosaurid *Liopleurodon* Sauvage, 1873 (Barrientos-Lara *et al*., 2015), the fish *Pleuropholis cisnerosorum* Alvarado-Ortega & Brito, 2016, as well as platychelyid remains, a sea turtle group present in the Caribbean region and South America (López-Conde, 2016; López-Conde *et al*., 2015), plus some ophthalmosaurid ichthyosaurs.

CONCLUSIONS

The present description of IGM 9026, the holotype of *Plesiosaurus mexicanus* and later tentatively referred as ?*Cricosaurus mexicanus*, shows enough tooth characters to support its unquestionable belonging to *Torvoneustes*. Given that IGM 9026 differs from the previous nominal species of this genus, we erected the new combination *Torvoneustes mexicanus*.

Despite of the collecting site of IGM 9026 was not well established, we consider the coincidence of three independent evidences to suggest their possible location and age. These evidences are: (i) the identification of IGM 9026 as a new species of *Torvoneustes*, previously known by two English nominal species recovered in Kimmeridgian strata; (ii) the hints left in the little geographical data of IGM 9026 provided by Wieland (1910); and finally, (iii) the recent discovery of a rich Kimmeridgian marine vertebrate assemblage in the Llano Yosobé showing the same preservation features of IGM 9026. We can now suggest that IGM 9026, holotype of *Torvoneustes mexicanus* (Wieland, 1910), could have been collected in the Kimmeridgian deposits of the Sabinal Formation.

The occurrence of *Torvoneustes* in the Tlaxiaco Basin is added to a growing number of vertebrates taxa that show taxonomical similarity between the Western and Eastern domains of the Tethys Sea.

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